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The strand flora of the Hawaiian Archipelago—II. Ecological relations

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TEMPERATURE

The Hawaiian littoral zone is characterized by relatively warm and uniform thermal conditions throughout the year. Sudden fluctuations are exceedingly rare and are never of great magnitude. The lowest recorded littoral temperature is 47° F., the highest is 98° F.; the mean of all littoral temperatures is 74° F. The mean monthly temperature at Honolulu, which may be taken as a representative coastal station, varies from about 70.5° F. to 76.8° F., in January and July respectively.

The following table, arranged from data of the Hawaiian Section, U. S. Weather Bureau, will show the temperature conditions (for 1915) of a number of littoral stations on the various islands. Data are not available from more strictly littoral stations—i. e., at the actual beach line itself. This is a problem that awaits future field investigation.

Station		Elevation in feet	Temperature		
			Mean	Max.	Min.
KAUAI:	Mana.....	30	73.9°	93°	51°
	Kealia.....	15	73.1	88	47
OAHU	Kahuku.....	25	76.6	88	60
	Honolulu....	111	75.0	87	58
	U. S. Mag. Sta.....	45	75.5	92	50
	Waianae.....	6	76.2	93	52
	Waialua Mill.....	30	74.3	93	52
MOLOKAI:	Kalawao.....	70	75.2	90	57
MAUI:	Kaanapali.....	12	72.8	91	55
	Haʻa.....	145	75.6	89	58
HAWAII:	Mahukona.....	11	75.5	98	58
	Niuhii.....	200	73.5	87	58
	Pepeekeo.....	100	73.3	86	57
	Hilo.....	100	72.6	87	54
	Kapoho.....	110	72.8	89	58

Olsson-Seffer ('10) presents data to show that on tropical and subtropical coasts the variations in the temperature of sea-water are mainly due to changes in the direction of the winds and cur-

rents. Close to the shore, or where the water is shallow, the temperature of the water is higher when the surface is calm, but low when the sea is rough. This is the natural consequence of the solar radiation in the former case, and of the mixing by the waves of the surface water with the cooler water from below when the sea is disturbed.

The annual thermal ranges of the oceanic waters of four representative regions will make a significant contrast with the conditions prevailing in Hawaiian waters: Sydney Harbor, Australia, 55.8°–72.4° F.; San Francisco Bay, California, 42°–69° F.; Woods Hole, Massachusetts, below freezing–70° F.; Plymouth, England, 44.1°–58.9° F.

The great oceanic current from the northeast, which travels down the Pacific Coast and out past Hawaii, as part of the Equatorial Drift, has so profound an effect upon the Hawaiian climate in general and the littoral zone in particular, that it merits special consideration here. Dr. Sereno O. Bishop, who made Hawaii his home for many years, writes ('04) of this current, as follows:

That remarkable stream of cold water, which flows in a vast stream southerly, skirting southeast Alaska, Vancouver's Island, the Pacific States of Washington, Oregon, and California, and finally passes out westward to Hawaii, beyond which group it becomes merged into the great equatorial current running westward.

This stream is of very low temperature, of immense volume, and of great velocity. It is unique in its powerful effects upon the climates of the coasts along which it flows. . . . Finally turning westward like the trade winds under the impulse of the earth's rotation, this mighty stream broadens out into the open ocean, gradually gaining warmth.

Dall ('04) states:

As it moves down the coast it loses its heat and produces the rain and fogs of the Oregonian region, cooling off so that when it reaches the latitude of the Golden Gate it has only the temperature of 54° or thereabouts, and is colder than the normal seawater for that latitude. It continues southward as a cold current, as described by Dr. Bishop. After traversing 2,200 miles it reaches the Hawaiian Islands, still at the low temperature of 70° in late summer, and of below 60° in late winter. This imparts to that favored group a uniformly subtropical climate such as is unknown to any other land in the same latitude.

Cowles, in describing the strand of the Lake Michigan dune region ('99, p. 107), states that on the beach, due to the "absence of vegetation and the general exposure . . . the temperature is higher in summer and lower in winter than in most localities. This great divergence between the temperature extremes is still

further increased by the low specific heat of sand." This is also true of the Hawaiian sand strands. There is a greater temperature range on the beach itself than in the protected zone lying immediately behind the beach. However, the temperature range of the littoral is insignificant when contrasted with that of the mountains that ascend directly from the lowlands, and in many places directly from the littoral. The diurnal range in temperature increases as one ascends the mountain slopes, and this range reaches its maximum on the high summits of Kea and Loa (nearly 14,000 ft.). Guppy ('03-'06) found the mean daily range of temperature on the summit of Loa, August, 1897, to be 30.6° F.; the lowest reading was 15° , the highest 61.2° .

Although sand has low specific heat, the upper dry layer becomes excessively hot under a cloudless sky. Cockayne ('11) records surface temperatures of 120° – 127° F. on the New Zealand strand; these figures are even higher than the generalization made by Guppy in the table given below. It should be noted, however, that the wet underlayers of sand absorb heat much more slowly. At the depth of a few inches below the surface the sand is always moist, so that the roots of sand-strand plants descend very quickly into relatively cool soil.

Guppy ('03-'06) makes the following generalizations concerning beach temperatures, the data applying to ordinary beaches under an unclouded sky, in the hot season, during the early afternoon:

			Surface—half-inch deep	Four inches deep
Temperate	about 50° – 55° lat.		100° – 105° F.	77° F.
Subtropical	" 30–35 "		105–110	80
Tropical	" 10–20 "		110–120	85

Olsson-Seffer ('09, pp. 88, 89) gives an extensive series of strand temperatures secured by him in various parts of the world.

With reference to temperature, Hawaiian strand regions may be classified as follows:

I. Warmer strands—leeward, facing SE., S., or SW.

1. Typical leeward beaches: e. g., Mana, Barber's Point, leeward Molokai, Lahaina, and Kawaihae.
2. Slope approaches plane perpendicular to incident sunlight: flat beaches, like those of Midway, Laysan, leeward Kauai and Puna.

3. Not subjected to shadows: as for 2.
4. Heat reflected by neighboring objects: e. g., Mana dune strand, Koko Head tufa cliff coast, Mokapu.
5. Composed of dark materials which absorb and retain heat: lava beaches of Hawaii, Maui, and parts of Oahu and Kauai.
6. Texture unfavorable for rapid evaporation of moisture: mud beaches and tufa cliff beaches, e. g., Pearl Harbor Inlet and Mokapu.
7. Arid or semiarid: not receiving the cooling effects of rain, waterfalls, etc., e. g., southwestern coasts of Maui and Hawaii.

II. Cooler strands—windward, facing NE., N., or NW.

8. All of the windward beaches.
9. Slope more or less precipitous: high beaches, e. g., Hamakua coast, windward East Molokai, Napali and Nihoa.

ILLUMINATION

The brilliant illumination of the Hawaiian strand is one of its most distinctive ecological features. The intense light of open beaches as contrasted with other regions, has been commented upon by ecologists in various parts of the world, but nowhere is this better exemplified than in the Hawaiian Islands. On the low islands the sky is cloudless, except during the infrequent rains. On the high islands the clouds heap over the mountainous interior, leaving the peripheral strand zone almost continuously exposed. The total insolation, in diurnal or in annual terms, is therefore exceedingly high. The Hawaiian coast, with its excessive insolation, may be contrasted, for example, with the gray, foggy coast of Washington and Oregon. On the coral and tufa beaches the intensity of the direct illumination is greatly increased by reflection. The glare on a coral beach, during the middle part of the day, as almost as intolerable to the eyes as that from a snow-field.

There are few data as to the direct and indirect effects of excessive insolation, save as an integral part of the xerophyte-producing complex. In general, light retards growth, and too great an intensity of light causes cessation of the growth of an organ. Pfeffer ('03, p. 87) states:

The internodes become shorter and the plant more condensed as the intensity of the light increases, while the leaves attain their maximal size at a certain medium intensity of illumination. This latter is owing to the fact that moderate light stimulates the growth of the leaves, whereas intense light retards it.

Jost ('07, p. 125) makes the following statements:

We are not accurately acquainted with the precise way in which assimilation is dependent upon the intensity of light. All researches agree on one point, viz., that assimilation of carbon is approximately proportional in amount to the intensity of light; it is questionable, however, whether this is the rule with higher intensities . . . it may be easily imagined that a further increase in assimilation, following on increase in light, is impossible owing to the deficiency in carbon-dioxide. Carbon-dioxide may be present in sufficient quantity under ordinary circumstances to employ all the energy of sunlight, but when light is artificially increased the usual amount of carbon dioxide would constitute a sub-optimum.

Schimper ('03, p. 58) states as a result of excess light;

Terrestrial plants . . . frequently suffer from a considerable disintegration of their chlorophyll. The vegetation of very sunny spots is never pure green, but always exhibits an admixture of yellow and brown tints due to the products of decomposition of chlorophyll . . . intense tropical light may even completely bleach the foliage.

Many of the Hawaiian beach plants are grayish or yellowish green. This is characteristic, not only of Hawaii, but also of other strands. As Cockayne ('11) suggests:

The yellow colour of certain dune plants belonging to different unrelated families is doubtless correlated with excess of light, and seems to me a possible example of heredity of an acquired character.

The author cannot share the latter view, as beach plants which have happened to grow in the shade develop normal green pigment, instead of the bleached beach pigment. Such species as *Santalum Freycenetianum* var. *littorale*, *Lepidium owaiense*, *Euphorbia cordata*, *Batis maritima*, *Argyrea tiliaefolia*, and *Cressa cretica* furnish excellent examples of this pronounced difference between the sun leaves and shade leaves of littoral plants.

A further comparison may be made which will illustrate the intensity of the strand illumination. In the rain-forest and summit-bog zones, and in the deep ravines of the lower and middle forests, the ordinary illumination on cloudy days—and these are regions of almost continuous cloudiness—necessitates a photographic exposure of say three minutes, whereas the same subject, distance, and aperture on the strand would require but one seventy-fifth of a second. The difference in illumination indi-

cated by these figures is thus about 13,500, that is, the beach illumination is approximately 13,500 times as great as that of the cloudy rain-forest. Of course, these figures do not include all of the light-factors involved, but they are sufficient to indicate the great differences in the illumination of regions not far removed from one another.

PRECIPITATION

All precipitation on the Hawaiian littoral occurs in the form of rain, dew, and rarely hail; snow is unknown. The strand is characteristically xerophytic or semi-xerophytic, as contrasted with the mesophytic lowland areas, and the montane rain-forests. The following data from representative stations of the U. S. Weather Bureau, 1915, will show these differences, the amount of rainfall being given in inches:

Island	Littoral station	Mesophytic station	Hygrophytic station
Kauai.....	16.98	38.02	75.52
Oahu.....	18.99	42.29	114.22
Maui (1914).....	20.91	42.70	397.26
Hawaii.....	8.41	39.10	159.60

A few littoral stations are mesophytic or hygrophytic, but this is a relatively unusual condition—e. g., Na Pali coast of Kauai, north coast of East Molokai, and Hamakua coast of Hawaii.

The relationship between the annual precipitation on the strand and the character of the vegetation is very close. The paucity of the Hawaiian arborescent strand flora is undoubtedly due in part to the xerophytic character of the littoral. In those few strand regions which do possess sufficient rainfall, the forest extends down to the beachline. The Puna, Hilo, and Hamakua regions, illustrate this condition. Schimper ('03, p. 407) makes the generalization:

Open littoral formations occur throughout the tropics, and in districts with a small rainfall they are almost the only ones. The close woodland above high-tide mark and the mangrove growing within reach of the tide are luxuriantly developed only in districts with abundant rain; and as the atmospheric precipitations decrease they become lower in stature, less close, and poorer in species.

In the case of the Hawaiian littoral vegetation, much emphasis must be laid upon the exterminating and limiting agencies which

have been introduced into the islands within historic times. The ravages of wild live-stock, such as cattle, goats, sheep, and swine; the clearing of the lowlands for agricultural and other purposes; the building of roads; the large quantities of firewood which were drawn from the nearest and most easily available sources; the introduction of a great variety of pernicious foreign weeds—all of these factors have contributed largely to the depletion of the lowland and littoral floras, and have given them an aspect of meagerness that they probably did not possess in their primitive state. Man and his domestic animals have been much more potent limiting factors than has been precipitation.

WIND ACTION

The wind is a powerful agency in its direct mechanical effects upon beach vegetation. Many strand plants have forms that are more or less protective, i. e., prostrate, creeping, rosette, or hemispherical aerial bodies. Plants of upright habit are permanently deflected and shaped by the wind; the windward branches are stunted and warped, and growth takes place chiefly on the leeward side of the plant. Seaside plants of *Acacia farnesiana*, *Prosopis juliflora*, *Santalum Freycinetianum* var. *littorale*, *Calophyllum inophyllum*, and *Kadua littorale* commonly illustrate this condition. These wind-beaten plants are invariably dwarfed.

The mechanical effect of the wind is greatly augmented on those coasts upon which it is able to pick up quantities of beach sand. At storm times, in such regions, the wind becomes a veritable sand-blast. The evidences of this sand-blast action, upon the trunks of both living and dead trees, and upon the local topography itself, are familiar to all who have travelled along a windy coast. The fantastic sculpturing of the seaward slopes of tufa in the Koko Head region, and at Mokapu Peninsula, admirably illustrate this sand-blast work. The herbaceous vegetation on these slopes is either prostrate or rosette, e. g., *Sesuvium Portulacastrum*, *Argyreia tiliaefolia*, *Boerhaavia diffusa*; or tough and wiry, e. g., *Sporobolus virginicus*, *Fimbristylis pycnocephala*.

On the Hawaiian littoral the wind is not as important an ecologic agent as in such a region as the Lake Michigan sand dunes. Here, according to Cowles ('99, p. 108), it "is the chief destroyer

of plant societies," acting in two ways—either by undermining plant individuals and groups, or by burying them with dune sand. Neither of these processes is particularly conspicuous along Hawaiian coasts; the vegetation is not sufficiently luxuriant to emphasize the former, nor are the dunes of sufficient size or mobility to give much importance to the latter. Here and there, however, both of these processes may be witnessed.

On the whole, the Hawaiian beach winds are retarding rather than destructive agencies. The Hawaiian strands may be divided into the following classes, based upon the relative exposure to wind action:

1. *Shores exposed to prevailing winds.*—The windward strands are much more exposed than are those along the leeward sides of the islands. Excellent contrasts are: the Hamakua and South Kona shores of Hawaii; the northeast and southwest shores of Haleakala; the north and south coasts of East Molokai; the Koolau and Waianae shores of Oahu; the Kilauea and Kekaha shores of Kauai.

2. *High or promontory-like shores.*—These are more exposed than are low flat shores. Good examples are: Hamakua, Hawaii; Hana and Kaanapali, Maui; the great pali of Molokai; Makapuu and Kaena, Oahu; Napali, Kauai; and the cliffs of Nihoa.

3. *Shores devoid of surface irregularities or vegetation sufficient to break the force of the wind.*—Low, flat shores, not protected by mountains behind them nor covered with forest, are exposed to the full force of the wind. In this class belong the coral atolls, and such shores as Kahuku and Mokapu, Oahu, the western extremity of Molokai, the Maui isthmus, and the extreme south point of Hawaii.

TRANSPIRATION

This is unquestionably the most important single physiological factor in determining the character of the Hawaiian strand flora. Only those plants which possess comparatively low transpiratory rates are able to permanently establish themselves upon the strand. Those species which invade the strand from the interior, and are characteristically mesophytic, undergo marked structural changes when they appear as members of the strand association.

The importance of the evaporation factor, particularly in the early stages of an association, is admirably emphasized by Transeau ('08, p. 230), who states:

The greatest decrease in the demands for transpiration on the part of seedlings takes place during the first stages. This greatly aids in accounting for the well-known fact that the development toward a closed association proceeds with such increasing rapidity when once a few plants gain a foothold. Attention has been frequently called to the importance of pioneers as shade-producers, while their effectiveness in reducing transpiration has been underestimated.

On the Hawaiian beaches a combination of factors—warmth, brilliant insolation, and exposure to powerful and rarely intermittent winds—tend to augment transpiration, and make of it an influence of great potency in retarding certain plants and completely inhibiting many others.

HAWAIIAN TIDES AS RELATED TO THE LITTORAL

On all oceanic coasts and embayments the tides exert an influence of greater or less power in determining the seaward limits of the land vegetation, and the landward extensions of the marine flora. In regions where the tidal range is great the effect upon the shore-line vegetation is proportionately augmented; in regions where the range is slight, its influence is small or negligible. The Hawaiian Archipelago comes under the latter class.

The greatest tidal contrasts in the Hawaiian Islands are due to coastal topography, i. e., sea-cliffs contrasted with mud-flats that lie only a few inches above low tide. At the foot of the sea-cliffs which rise directly from the water is a tidal (and wave-splash) zone of two or three feet. This zone is conspicuously marked by the coralline algae, which form a reddish-purple or lavender band. If conditions for land-plants are favorable, they may occur only a few feet above this zone, within reach of the salt spray, and from a distance appear to rise from the sea itself. Plant-clad cliffs of this character also occur in many of the South Pacific islands.

The mud-flats, however, present broad, rocky, mud-covered platforms, a few rods to a half-mile in width, almost free from seawater at low tide, but covered at high tide with six to twenty-four inches of water. The land vegetation is restricted to the shoreward limits of these flats. The absence of the land-building halophytes—*Rhizophora*, *Bruguiera*, *Cerriops*, *Kandelia*, etc.—makes invasion very slow.

The mean range of the Hawaiian tides is very slight, that at Honolulu being 1.3 feet, and that at Hilo, 1.8 ft. These ranges are typical for all the islands, and contrast forcibly with the large ranges of many other littorals. For example at Apia, Samoa, the average rise is 3 ft. per tide; the tides in Sydney Harbor rise 6-7 ft.; Johnson and York ('15, p. 131) in their comprehensive ecological study of the tide-levels at Cold Spring Harbor, New York, found a mean tidal range of 7.63 ft., with a variation of from 4.2 ft. to 10.8 ft.

The following data from the U. S. Coast and Geodetic Survey Tide Tables show the tidal range through a single typical month, January, at Honolulu, in feet:

Date	Moon	1	2	3	4
3	New; farthest south.....	2.2	0.1	0.6	-0.2
4	Perigee.....	2.3	0.1	0.6	-0.1
9	Equator.....	0.5	1.4	0.0	1.0
10	First quarter.....	0.7	1.2	0.0	1.2
16	Farthest south.....	2.1	0.2	0.6	-0.1
18	Full moon; apogee.....	2.1	0.2	0.6	-0.1
24	Equator.....	0.4	1.3	0.0	1.1
26	Third quarter.....	0.7	0.9	0.0	1.5
30	Farthest south.....	2.1	0.2	0.7	-0.2

Contrasting sharply with the poorly defined tidal zones of the Hawaiian littoral are those regions with large tidal fluctuations. For example, Ganong ('06, p. 85) in his studies of the Miscou Island littoral, in the extreme northeast corner of New Brunswick, on the Gulf of St. Lawrence, found three well defined beach zones:

First—"a broad sloping inter-tidal beach of pure sand without vegetation." This corresponds to the mud-flats along the southern shores of Oahu.

Second—a "narrow band between ordinary and extreme high tides." This zone was practically barren of vegetation. This zone is negligible in Hawaii.

Third—a "broad shelf, . . . reached only by the very highest tides." This is an "upper beach," and is characterized by scattered drift-wood and dry, ever-shifting sand. Some of the typical plants of this zone are *Salsola Kali*, *Cakile edulenta*, *Atriplex patula hastata*, and *Ammophila arenaria*. Ganong states "that

this vegetation is distinctly adjusted to the physical conditions, for it is of great paucity, of small and slow growth, annually renewed, closely ground-appressed, and strongly xerophytic."

Brownlie ('02) makes much of the irregularity of the tidal intervals in the Pacific, and states that at Honolulu the intervals of time from one high water to the next vary from ten and three-quarters to thirteen and three-quarters hours. A range so wide apart shows great irregularity compared with the absolute regularity of the movements of the moon. Although this tidal phenomenon is of great significance from the standpoint of tide studies themselves, it is not a factor of any special importance in the littoral ecology of land-plants.

Although the Hawaiian marine flora is closely limited by tidal intervals, these intervals are of little significance in determining the zonation of land-plants, as compared with the importance of other ecological factors. This contrasts with the findings of Johnson and York ('15, p. 149), at Cold Spring Harbor, who state:

A careful study of the vertical distribution of the littoral plants about this harbor shows that this depends primarily and very definitely on the relative time of their submergence and emergence with the rise and fall of the tide. Moreover, the vertical range of littoral species is strictly, sometimes very narrowly limited. There are no species here, except two or three algae, that are distributed "between tidemarks" (*i. e.*, from low water up to high water), as is so often reported. The nearest approach to this range found for any seed plant is that of *Spartina glabra*.

It must be noted that the above statement uses the term littoral in a relatively narrow sense, as does their further statement that the vertical range of a littoral plant is exactly proportional to the range of the tide. This does not apply to the customary usage of the term littoral, which includes all vegetation along the coasts or strands, the ranges of which are more or less closely maritime.

NATURE OF THE SUBSTRATUM

The character of the littoral substratum obviously plays an important rôle in determining the nature and distribution of the littoral flora. Warming ('09, p. 223) groups halophytic plants into four classes, according to the nature of the substratum upon which they reach their optimum development: lithophilous, psammophilous, pelophilous, and helophilous. This will serve as a convenient basis for classifying the Hawaiian strand, with the

reservation that not all strand plants are halophytes. The Hawaiian types to be considered may be referred to the lithophilous and psammophilous classes, as follows:

A. LITHOPHILOUS

1. Sheet or flow lava.
2. Vertical rock shores or sea cliffs.
3. Littoral creviced rocks.
4. Lava boulder and pebble beaches.
5. Tufa beaches.
6. Coral limestone strands.

B. PSAMMOPHILOUS

7. Coral sand.
8. Root molds.

1. *Sheet or flow lava*.—This type of strand is of first importance in the Hawaiian group, both quantitatively and from the standpoint of ecologic history. There are more miles of lava beach than of any other type, or of all the other types combined. The relatively large areas and recent formation of Maui and Hawaii have caused this to be the dominant type. Historically it is first to appear, and it eventually gives way to strands of other types. The lava flows may be either relatively recent and uneroded, like many on the island of Hawaii, or they may be of extreme antiquity and deeply carved, like those of the Na Pali coast of Kauai, or Kaena and Makapuu, on Oahu. The beach itself, in either case, is formed of exposed lava beds, very rocky, with practically no sand or soil, and distinctly uncongenial to plant life. Lava sheet beaches occur on all the larger islands, but are best exhibited on the shores of Hawaii and East Maui. Every gradation may be found from very low, flat lava strands, only a few feet above sea-level, to bare sea precipices 600–700 feet in height.

From the historic standpoint the lava beach is of twofold significance. If of recent flow material—e. g., the Hawaii flows of 1840, '59, '68, '87—it indicates the extinction of the vegetation which occupied the old strand, and the exposure of a new littoral surface to plant invasion. On the other hand, in the early geo-

logical history of the islands the Hawaiian strand was wholly of sheet lava, and today remnants of this primitive beach condition exist here and there along the coasts. Thus there is great diversity in the ages of the various shores, and in the amount of plant invasion, both from within and from without, to which they have been exposed.

2. *Vertical rock shores or sea cliffs*.—These are composed either of sheet lava or laminated tufa. They are produced by sea action and fracture. Some of the stupendous sea-cliffs of Hawaii, Molokai, and Kauai, may have been produced by volcanic or seismic activity. The sea-cliffs either rise sheer from the water, or have a narrow strand at the base; this depends upon the depth of the off-shore water and both conditions are of frequent occurrence. None of the sea-cliffs, no matter how precipitous or apparently uncongenial for plant life, are wholly devoid of vegetation. Here and there on the surface of the cliff are crevices, ledges, and little pockets where plants establish themselves.

On the arid precipices—e. g., Koko Head, Makapuu, Mokapu and Kaena—occur such plants as *Euphorbia cordata*, *Lepidium owaiense*, *Schiedea globosa*, *Kadua littoralis*, *Tetramolopium* spp., *Lipochaeta integrifolia*, *Gossypium tomentosum*, *Sida* spp., *Jacquemontia sandwicensis*, *Boerhaavia diffusa*, *Cassia Gaudichaudii* and *Capparis sandwichiana*.

On the humid sea-cliffs—e. g., Waipio, Nahiku and East Molokai—are such forms as *Campylothea molokaiensis*, *Schiedea Lydgatei*, *Lysimachia spathulata*, *Metrosideros polymorpha*, *Tribulus cistoides* and *Nama sandwicensis*.

3. *Littoral creviced rocks*.—Along the lava flow and tufa-cliff coasts, and to a lesser degree along the uplifted coral limestone shores, the rock crevices are the special habitats of many strand plants. The crevices are of two kinds: those due to the lamination of the rock, that is of the sheets or layers of lava or tufa; and those due to the vertical faulting of these layers. The former condition produces horizontal crevices, which on the sea-cliffs often front on ledges of greater or less magnitude. The vertical checking and faulting produces numberless irregular crevices upon the surface of the exposed strata, and in these crannies soil, seeds, and spores are lodged. Many of the crevices are less than an inch in

width, and the plants grow on top of the crevice, merely rooting in it. Others are several inches wide, and the smaller plants, such as *Lipochaeta succulenta*, *Lepidium owaihense*, and *Cressa cretica*, grow down within the crevice, only the upper parts of the branches showing above the rock. In the very large fissures,—one to three feet wide, the entire plant body may be concealed within the fissure.

4. *Lava boulder and pebble beaches*.—Wherever the shore line lava-sheets are subjected to the action of the sea, they are gradually broken into massive boulders, which in turn are slowly ground into pebbles. These metamorphoses are abundantly illustrated along the windward coasts of Hawaii, Maui, and Molokai, and in such places as Kaena, Oahu, and Kilauea, Kauai.

The boulders are usually 2–3 ft. in diameter, more or less oblate, smooth, black, very hard, heavy, and resonant. A beach composed of these ponderous rocks is very impressive, particularly during storm time, when the sea mills them with irresistible power. In various places, especially on the coasts of Kauai and Oahu, the lava boulders are consolidated in a calcareous matrix, formed of re-deposited coral lime.

The seaward portion of a boulder beach is barren of terrestrial vegetation, as is to be expected, but the upper or landward portion, which is not disturbed by ordinary wave action, is the habitat of such forms as *Sesuvium Portulacastrum*, *Ipomaea glaberrima*, *I. insularis*, *Euphorbia cordata*, *Tetramolopium* sp., *Kadua littoralis*, and *Wikstroemia Uva-ursi*.

The pebble beaches are relatively uncommon on Kauai and Oahu, but are more common on Maui and Hawaii. The pebbles, at the upper margin of the beach, are intermingled with soil, and the line of demarcation between beach and lowland is not distinct.

5. *Tufa beaches*.—Tufa craters occur here and there throughout the islands, from sea-level up to the highest mountain summits. In a few instances tufa cones stand so close to the shore line that the sea has cut beach platforms in their slopes. In these cases the strand is made of the solid wave-cut tufa rock. Leahi, Koko Head, Koko Crater, Manana, and Mokapu, illustrate this condition. The tufa is soft and easily sculptured by the waves; it usually does not form boulders or pebbles, but fractures easily and

disintegrates into mud. The main part of the tufa platform is wave-swept and barren of vegetation; the upper portion is the habitat of such forms as *Nama sandwicense*, *Sicyos hispidus*, *Jacquemontia sandwicensis*, *Tribulus cistoides*, *Cenchrus calyculatus*, *Waltheria americana*.

Tufaceous sand or mud is brownish or yellowish green in color, much finer in texture than the coral sand, and much more retentive of moisture. It often contains large quantities of olivine; this imparts the greenish hue. Some common plants of the muddy beaches are: *Batis maritima*, *Polypogon littoralis*, *Thespesia populnea*, *Ruppia maritima*, *Cyperus laevigatus*, *Chenopodium album*.

A number of small islets, such as Moku Manu, Manana and Molokini, are made up largely or wholly of tufaceous deposits, and represent the eroded remains of former tufa cones.

6. *Coral limestone strands*.—Within recent geological times there has been a slight uplift at various points in the Archipelago, which has resulted in elevating above sea-level broad shelves of coral limestone. Such areas are especially abundant on the island of Oahu, and portions of the shore around Pearl Harbor, Kaneohe Bay, Waianae, Kahuku, and Barber's Point are formed of the exposed coral limestone. These shores are often undercut by the surf, and are sculptured from above by the action of rain-water. The limestone along the beach may be actually wave-washed, or may be more or less buried beneath coral sand. Further back from the shore it is usually covered with a layer of soil.

7. *Coral sand*.—Beaches of pure coral sand are abundant on the islands of Oahu and Kauai, and also occur on the islands of Maui and Molokai. On the coral atolls to the leeward the coral strand is, of course, dominant. The sand is washed ashore from the coral reefs, and sometimes accumulates in sufficient quantities to form dunes. Mana, Kauai, Makaha and Heleloa, Oahu, and West Molokai, are representative dune regions. Fine stretches of coral beach may be found at Waikiki, Makapuu, Waimanalo, Mokapu, Kanuku, Waianae, and Ewa.

The Hawaiian coral strands correspond to the xerophytic beaches of Cowles ('99, p. 112), who recognizes two classes of beaches: hydrophytic and xerophytic, defining the latter as essen-

tially a product of wave action and comprising the zone which is or has been worked over by the waves. Hence the beach may be defined as the zone between the water level and the topographic form produced by other agents. This definition is closely applicable to the Hawaiian coral sand beaches, which are uniformly xerophytic in their characteristics. Olsson-Seffer ('10) has stated that the competition for food is more intense, the water supply less, the light stronger, the temperature higher, the transpiration greater, the foothold more uncertain and difficult, the conditions for plant life generally more adverse, than on any other soil.

Shaler ('94) has made some significant generalizations concerning sandy beaches. He points out that dunes and beaches of coral sand never march far inland, as do quartz sand dunes, for the reason that the limestone grains speedily become consolidated into a tolerably firm set rock. It is characteristic of coral beaches that the materials of which they are composed, unlike those of ordinary shores, are readily taken into solution, and in that state may be borne away by the currents to any distance. Notwithstanding the constant robbery of their materials, which is effected by the solving process, the coral beaches often widen with great rapidity. Shaler emphasizes that one of the most noticeable features which is exhibited by beach sands is their extraordinary endurance of the beating of the waves. He compares the rapid abrasion of rocks and boulders to the very insignificant abrasion of sand particles. Though subjected for ages to the beating of the waves, with perhaps a hundred times as much energy applied to the surface of which it forms a part as would suffice to reduce a granite boulder containing a cubic foot of material to a granular or powdery state, the beach sand remains unworn. This endurance is due to the capillary water. So long as the beach is full of water the particles do not touch each other. Thus the blow of the waves is used up in compressing the interstitial water and is converted into heat without wearing the mineral matter in an appreciable degree.

Sandy beaches have a relatively slight water capacity, as the percolation is very rapid. The capillarity is not as pronounced as in soils of finer texture, and the evaporation from a sandy surface

is quite rapid. All of these conditions tend to greatly reduce the available water supply of a beach, even though the latter be exposed to normal precipitation. In other words, the physical characteristics of the sandy beach, as has already been suggested, tend strongly toward xerophytism. Olsson-Seffer ('10) shows that it is the volume of water which a soil is capable of placing at the disposal of the plant, which is the limiting factor in the production of its vegetative covering and the controlling condition in the distribution of this vegetation. Percolation in sand is so rapid that were it not for the counteracting influence of surface tension very little water would be retained by sand. Permeability increases as the sand particles increase in size. Internal dew formation in the sand is the direct cause of a portion of the permanent moisture of the strand or dune. It is also to be noted, in this connection, that extreme changes in the salinity of the soil water, due to flooding by fresh water, are detrimental to the strand flora.

The two important constituents of the soil water of the sandy beach are lime and salt. On coral beaches the percentage of lime is very high. It is dissolved out by the rain-water, and ultimately forms consolidated limestone. The soluble salt content is coastal and is not of as great ecologic importance as was formerly supposed. An excellent statement is given by Olsson-Seffer ('10). Sandy soil yields its water to plants more freely than do other soils, and below the superficial layer of dry sand there is always a surprising amount of water. Fuller ('12) found this to be more than double the wilting coefficient of dune soil.

Owing to the frequent inundations by waves and subsequent rapid changes in evaporation, the soil temperatures of the lower sand beach are more variable than on any other formations of the sandy strand. On account of the low specific heat of sand, the surface layers are rapidly heated in the daytime and quickly cooled at night. Thus there is considerable fluctuation of diurnal temperatures.

The list of plants enumerated by Schauinsland ('99) as occurring on the Laysan atoll may be taken as representative of the coral strand flora of the leeward isles. This list includes:

<i>Lepidium owaiihense</i>	<i>Phyllostegia variabilis</i>
<i>Capparis sandwichiana</i> *	<i>Boerhaavia diffusa</i>
<i>Portulaca oleracea</i>	<i>Achyranthus splendens</i>
<i>Tribulus cistoides</i>	<i>Euxolus viridis</i>
<i>Sicyos hispidus</i>	<i>Chenopodium sandwicheum</i>
<i>Sicyos microcarpus</i>	<i>Santalum Freycinetianum</i>
<i>Sesuvium Portulacastrum</i>	<i>Cyperus laevigatus</i>
<i>Lipochaeta integrifolia</i>	<i>Cyperus pennatus</i>
<i>Scaevola Lobelia</i>	<i>Cenchrus calyculatus</i>
<i>Solanum laysanense</i>	<i>Sporobolus virginicus</i>
<i>Ipomoea Pes-caprae</i>	<i>Eragrostis hawaiiensis</i>
<i>Ipomoea insularis</i>	<i>Lepturus repens</i>
<i>Nama sandwicensis</i>	<i>Pritchardia Gaudichaudii</i>
<i>Heliotropium curassavicum</i>	

8. *Root-Molds*.—An interesting formation along the Hawaiian littoral, that has also been recorded from other parts of the world (see Dolley, '89, pp. 131, 132; and Darwin, '60), is the root-mold. This is well developed on sandy shores with persistent winds, where there has been considerable vegetation. The west end of Molokai, the Maui isthmus, Makapuu and Kaena on Oahu, and the Mana region of Kauai all possess notable root-mold formations. The molds are produced by the cementing together of the sand particles which lie near the ramifying roots of beach plants; the cementing process is undoubtedly due to specific root excretions, as well as to the percolating rain-water which follows the courses of the larger roots. In the course of time the vegetation dies, the winds sweep away the loose sand from around the more solid molds, and the latter are eventually exposed. They appear either as isolated cylinders, rising here and there above the sand, or as irregular masses of branching tubes. They rise to a height of three to twenty inches above the present level of the sand, and in color are white or yellowish brown.

The lumen varies from a fraction of an inch to nearly a foot and is rarely open; it is more or less completely filled with limestone. The smaller sizes are the most common, as the majority

* This abundant indigenous pseudolittoral was inadvertently omitted from the list on p. 276. It is a straggling shrub, inhabiting arid rocky lowlands and beaches; a favorite habitat, for example, is a rocky talus slope near the sea.

of beach plants are slender-rooted. Upon close examination the wall is found to be composed of sand, coral particles, and other minutiae compactly cemented together. In cross section the wall shows a very much hardened inner layer forming a distinct zone. The outer layer is relatively soft and easily crumbled.

These molds are the fossils of the root-ramifications of a previous plant formation. Molds identical in mode of formation with those of the coral strands are also plentiful in the tufa slopes, and attain much larger sizes than the sand molds. Punchbowl, Round Top, Diamond Head, and Koko Head are typical regions where these molds occur in abundance and in all stages of development.

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